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REVIEW

Emotional behavior in aquatic organisms? Lessons from crayfish and zebrafish

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Abstract

Experimental animal models are a valuable tool to study the neurobiology of emotional behavior and mechanisms underlying human affective disorders. Mounting evidence suggests that various aquatic organisms, including both vertebrate (e.g., zebrafish) and invertebrate (e.g., crayfish) species, may be relevant to study animal emotional response and its deficits. Ideally, model organisms of disease should possess considerable genetic and physiological homology to mammals, display robust behavioral and physiological responses to stress, and should be sensitive to a wide range of drugs known to modulate stress and affective behaviors. Here, we summarize recent findings in the field of zebrafish- and crayfish-based tests of stress, anxiety, aggressiveness and social preference, and discuss further perspectives of using these novel model organisms in translational biological psychiatry. Outlining the remaining questions in this field, we also emphasize the need in further development and a wider use of crayfish and zebrafish models to study the pathogenesis of affective disorders.

KEYWORDS
aggressiveness, anxiety, crayfish, social preference, translational research, zebrafish

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1 | INTRODUCTION

Proper responses of animals to stress are critical for their survival, however maladaptive responses may also become pathological, resulting in social and affective disorders (Campos, Fogaca, Aguiar, & Guimaraes, 2013; Nuss, 2015). Animal experimentation has been an indispensable tool for understanding the neurobiological bases of stress and how it connects with emotional responses (Belzung & Lemoine, 2011; van der Staay, 2006). An emotional response has subjective, behavioral, and physiological components and, while the former is fundamental for human experience, the latter two can be studied in animals (Oatley & Johnson-Laird, 2014), including both vertebrate and invertebrate species (Baracchi, Lihoreau, & Giurfa, 2017). Considering that shifts in emotional response are a crucial component of many mental disorders and that the translatability of current studies is still limited, additional and more focused studies are needed to ultimately contribute to understanding these disorders, including widening the spectrum of species used in the central nervous system (CNS) disease modeling (de Mooij-van Malsen, Vinkers, Peterse, Olivier, & Kas, 2011; Kas et al., 2011; Maximino et al., 2015; Stewart et al., 2015; van der Staay, Nordquist, & Arndt, 2017). Clearly, the choice of model organisms from other taxa beyond mammals is a challenging task driven by numerous considerations (Maximino et al., 2015). To increase the translatability of such tests, their ethological, ecological and evolutionary aspects must be considered to ensure construct validity (Kas et al., 2011; Maximino, de Brito, Dias, Gouveia, & Morato, 2010; Maximino & van der Staay, 2019).

A broader knowledge of behavioral biology of model organisms is critical, and must consider the natural habitat, movement preferences and the overall distribution of organisms in ecological contexts (Benvenuto, Gherardi, & Ilheu, 2008; Brown, Laundré, & Gurung, 1999; Ferrari, Sih, & Chivers, 2009; Laundré, Hernández, & Ripple, 2010). In rodents, this approach has already been widely used to support the choice of specific behavioral models and tests (Blanchard & Blanchard, 1988; Hånell & Marklund, 2014). Complementing rodent models, some aquatic vertebrate (e.g., zebrafish, *Danio rerio*), and invertebrate (e.g., crayfish) models have recently emerged to improve our understanding of emotional-like states under normal and pathological conditions (Fossat, Bacqué-Cazenave, De Deurwaerdère, Cattaert, & Delbecque, 2015; Maximino et al., 2015). Studies focusing on these models reveal some comparative relevance to humans (Fossat et al., 2015; Fossat, Bacqué-Cazenave, De Deurwaerdère, Delbecque, & Cattaert, 2014; Gerlai, 2014; Stewart, Braubach, Spitsbergen, Gerlai, & Kalueff, 2014), with the advantages of having a shorter generational time that potentially enhances the detection of developmental (e.g., drug/toxin) and transgenerational (e.g., genetic and epigenetic) effects (Imeh-Nathaniel, Orfanakos, Wormack, Huber, & Nathaniel, 2019; Lakstygal, de Abreu, & Kalueff, 2018; Scholtz et al., 2003; Spence, Gerlach, Lawrence, & Smith, 2008). Here, we call for a wider use of aquatic organisms, such as zebrafish and crayfish, for modeling stress, anxiety, aggressiveness and social preference deficits. As we discuss crayfish and zebrafish stress-related behaviors, we also critically evaluate their utility for probing neural underpinnings of anxiety, aggression and social preference.

Significance

Mounting recent evidence suggests that aquatic organisms, including both vertebrate (e.g., zebrafish) and invertebrate (e.g., crayfish) species, may be relevant to studying emotional behavior and its deficits. These model organisms possess considerable genetic and physiological homology to mammals, display robust behavioral and physiological responses to stress, and are sensitive to various drugs known to modulate stress and affective behaviors. Here, we summarize recent findings in the field of zebrafish- and crayfish-based modeling of stress, anxiety, aggressiveness and social preference, and discuss further perspectives of using these novel model organisms in translational biological psychiatry.

2 | BEHAVIORAL ECOLOGY OF CRAYFISH AND ZEBRAFISH

Crayfish include >540 Decapoda species belonging to three families (Crandall & Buhay, 2008)—*Astacidae* (native to Western North America and Europe), *Parastacidae* (native to the Southern hemisphere), and *Cambaridae* (inhabiting the East of the Americas) (Shen, 2008). Found in freshwater environments (e.g., lakes, reservoirs and streams), crayfish tend to burrow or hide under rocks or other shelters to avoid their natural predators (Rhoades, 1962), such as fish, birds and mammals (Delibes & Adrián, 1987; Holdich, 1988). Generally, crayfish are social animals and form overt social dominance (Figler, Finkelstein, Twum, & Peeke, 1995; Issa, Adamson, & Edwards, 1999). Mostly nocturnal and crepuscular species (Holdich, 2001), their locomotion is characterized by short peaks of intense crawling alternated with periods of low mobility (Anastácio et al., 2015; Aquiloni, Ilhéu, & Gherardi, 2005; Francesca Gherardi & Barbaresi, 2000; Gherardi, Barbaresi, & Salvi, 2000). In particular, crayfish (*Procambarus clarkii)* is an omnivore species that feeds on plant and animal detritus, macrophytes and small live animals (e.g., molluscs, insects, annelids, nematodes, platyhelminthes, tadpoles and fingerlings) (Loureiro, Anastácio, Araujo, Souty-Grosset, & Almerão, 2015). The genome of this species contains nearly 137 thousand genes and 152 thousand predicted exons, ranging from 150 to 12,807 bp in length (Shi, Yi, & Li, 2018).

Zebrafish is a small teleost fish species, native to Southeast Asia, that typically inhabits shallow slow-moving streams, small rivers and especially still pools formed during the monsoons (Engeszer, Patterson, Rao, & Parichy, 2007; Parichy, 2015). Their most common predators include other fishes (e.g., snakeheads [*Channa spp.*], Indian Leaf fish [*Nandus nandus*] or freshwater garfish [*Xenentodon cancila*] [Bass & Gerlai, 2008; Engeszer, Patterson, et al., 2007]), birds, and

insects (e.g., dragonfly larvae [Spence et al., 2006]). Zebrafish is a highly social species whose innate shoaling behavior (Engeszer, Da Barbiano, Ryan, & Parichy, 2007; Engeszer, Patterson, et al., 2007) involves synchronized, ordered group swimming (Delcourt & Poncin, 2012) that aims to increase the probability of an individual fish detecting/avoiding predators (Pitcher, 1983).

The overlapping ethological and habitat characteristics of these two aquatic species may provide an opportunity to use their natural antipredator and social behaviors (including avoidance, aggression and other conspecific interactions) to develop behavioral assays enabling the study of basic aspects of affective behavior, including anxiety, aggression and sociality. Recognizing the growing value of widening the spectrum of model organisms in translational affective research (Kalueff, Stewart, & Gerlai, 2014; Stewart, Braubach, Spitsbergen, Gerlai, & Kalueff, 2014), it is timely to consider using aquatic models, such as crayfish and zebrafish, to examine emotionality-related traits. On the one hand, such use of invertebrate and anamniote model organisms may help bridge important evolutionarily-based gaps in our understanding of the neural underpinnings of normal and pathological behavior (Fossat et al., 2015; Maximino et al., 2015). On the other hand, this approach may also increase the overall translatability of neurobehavioral models, given that mechanisms shared between rodents, zebrafish (Gerlai, 2014; Stewart, Braubach, Spitsbergen, Gerlai, & Kalueff, 2014) and, possibly, crayfish (Fossat et al., 2014, 2015), are likely to represent "core" pathways shared with humans. Thus, this strategy may further support innovative cross-species modeling (Kas et al., 2011), based on both vertebrate and invertebrate species, for studying basic, evolutionarily conserved, aspects and neural underpinnings of affective behaviors.

3 | MEASURING AFFECTIVE-LIKE BEHAVIOR IN CRAYFISH AND ZEBRAFISH

3.1 | Stress/anxiety-like behavior

Stress-related behavior has been studied in the red swamp crayfish (*P. clarkii)* (Hobbs, 1972), a native to Mexico and South-Central USA. Since crayfish naturally explore new environments and (like rodents) prefer the dark (Yamane & Takahata, 2002), their anxiety/avoidance-like behavior can be assessed in the light-dark plus maze consisting of two shaded "dark" and two open "light" arms (Figure 1; Bacqué-Cazenave, Cattaert, Delbecque, & Fossat, 2017; Fossat et al., 2014, 2015). Stressing crayfish by an electric shock (Fossat et al., 2014, 2015) or descending their social status (Bacqué-Cazenave et al., 2017) increases preference for the dark arms (Table 1). Their sensitivity to benzodiazepines (Bacqué-Cazenave et al., 2017; Fossat et al., 2014) suggests some predictive validity of the model (e.g., similarity of drug effects with clinical treatment in humans) despite major neuroanatomical differences from mammals.

The three most commonly used anxiety tests in zebrafish are the novel tank test (or novel tank diving test, NTT), the open field test (OF), and the light-dark test (LDT) (Figure 1; Kysil et al., 2017). Other anxiety screens include the plus-maze with ramps (Varga et al., 2018; Walsh-Monteiro et al., 2016), the novel object approach (Fior et al., 2018; Johnson & Hamilton, 2017), and inhibitory avoidance tests (Blank, Guerim, Cordeiro, & Vianna, 2009; Gorissen et al., 2015; Manuel et al., 2014). Zebrafish NTT is based on geotaxis, an innate escape 'diving' behavior in novel environments, where zebrafish initially spend more time at the bottom and exhibit more erratic movements and freezing/immobility (Bencan, Sledge, & Levin, 2009; Cachat, Stewart, et al., 2010; Egan et al., 2009). Such natural diving response is generally expected from zebrafish, as in the wild they inhabit shallow pools where their main predators—fish or birds—would attack from the side or the top (Parichy, 2015). However, due to habituation to the NTT apparatus with the lack of overt danger, zebrafish gradually (within minutes) begin to explore the top area (Stewart et al., 2013; Wong et al., 2010). A typical NTT represents a transparent narrow rectangular tank virtually divided into two (top and bottom) or three areas (bottom, middle, and top) (Egan et al., 2009; Kysil et al., 2017). This test assesses three major phenotypic domains: exploration of novel environments (time spent in the upper/bottom zone, latency to enter the top, number of crossings between the zones), fear-like behavior (e.g., freezing and erratic swimming), and overall activity/locomotion (e.g., distance traveled and velocity; Cachat, Stewart, et al., 2010).

Like in rodents, zebrafish NTT behaviors can be explained by a classical motivational conflict theory (Montgomery, 1955) based on a balance between anticipation of potential threats versus exploration (Davis, Walker, & Lee, 1997; Maier, 1993) and also by the avoidance theory viewing animal novelty-evoked behavior as driven by avoidance responses (e.g., avoiding potentially dangerous areas) (Gallup, 1974, 1979; Wallnau & Gallup, 1977). Finally, while rodent studies suggest that neural circuits of fear may differ from those involved in anxiety (Davis et al., 1997), this distinction remains unclear in fish models. However, as NTT responses are highly sensitive to anti-anxiety drugs (Stewart, Wu, et al., 2011), this suggests a reasonable predictive validity in this assay.

The OF is another popular test to assess animal affective-like behavior. In rodents, the OF apparatus typically consists of a circular or rectangular arena (Denenberg, 1969; Harro, 2018) to measure locomotion (e.g., the number of squares crossed or total distance traveled) and anxiety-like center avoidance (e.g., entries or time spent in center vs. periphery). Stressed/anxious animals decrease the exploration and increase time spent in the periphery of the apparatus (thigmotaxis) (Denenberg, 1969; Harro, 2018). Similar to rodents, both larvae and adult zebrafish display characteristic patterns of exploration, with prominent thigmotaxis (Ahmad & Richardson, 2013; Stewart, Gaikwad, Kyzar, & Kalueff, 2012), suggesting that spatiotemporal strategies of exploration may be evolutionarily conserved across vertebrate species (Stewart et al., 2012).

The zebrafish LDT is based on the natural tendency of fish to display scototaxis, avoiding brightly lit areas and spending more time in the dark to minimize their detection by predators (Maximino, De Brito, de Mattos Dias, Gouveia, & Morato, 2010; Serra, Medalha, & Mattioli, 1999). The typical LDT apparatus is a rectangular tank consisting of two equal vertical portions, black and white (Maximino,

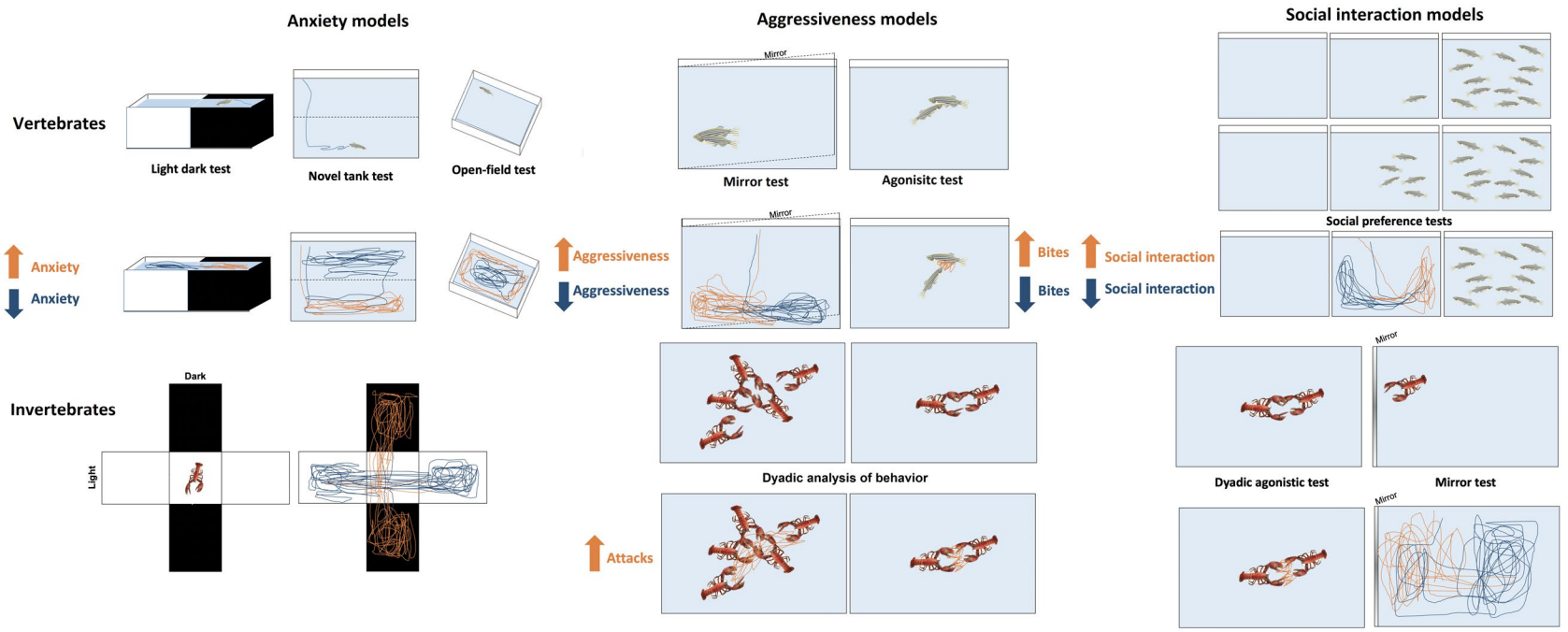

FIGURE 1 Selected behavioral tests used to assess anxiety, aggressiveness and social preference in zebrafish and crayfish. The line traces represent increased (orange) or decreased (blue) respective behaviors in these species [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Selected examples of pharmacological modulation of crayfish behavior

Drugs	Dose	Behavioral effects	References
Aggression			
5-Hydroxytryptophan (5-HTP) and fluoxetine	100 mg/kg 5-HTP, or 100 mg/kg 5-HTP + 0.31 mg/kg fluoxetine	Increased aggression in 5-HTP versus 5-HTP + fluoxetine subordinates	Dingman, Hurlburt, and Otte (2009)
Crustacean hyperglycemic hormone (cHH)	0.5 μg per crayfish	Increased individual aggression	Aquiloni, Panksepp, and Huber (2012)
Anxiety			
Chlordiazepoxide	15 μg/g	Prevented stress effects of electric shocks, anxiolytic effect	Fossat et al. (2014, 2015)
Serotonin (5-HT)	5 μg/g	Anxiogenic effect	Fossat et al. (2015)
Mianserin and methysergide[a]	1 nmol/g	Reduced anxiogenic effects of 5-HT	Fossat et al. (2015)
D-amphetamine	1 and 5 mg/kg	Increased exploration (e.g., antennal movements, rearing, and locomotion)	Alcaro et al. (2011)
Social preference			
Anisomycin	0.1 ml saline solution	Increased agonistic behavior in the dyadic test	Jiménez-Morales et al. (2018)
Scopolamine	100 ng/g	Increased agonistic behavior in the dyadic test	Jiménez-Morales et al. (2018)

[a]Mianserin is a serotonin 5-HT2 receptor blocker, and methysergide is a 5-HT1/2 receptor blocker.

De Brito, et al., 2010). In this test, anxiogenic-like effects include more time spent in the dark (Maximino, De Brito, et al., 2010), in addition to risk assessment (defined as partial or very fast entries in the white compartment, during which the animal gathers information on threat levels), thigmotaxis (swimming near the walls of the tank), freezing (cessation of swimming and most movements), and erratic swimming (a zig-zagging, fast pattern of swimming in which the animal's direction is unpredictable to predators) in the white area (Araujo et al., 2012). Interestingly, the characterization of anxiety in the LDT paradigm is age-specific, as for instance, larval fish display natural dark avoidance (Steenbergen, Richardson, & Champagne, 2011) that is attenuated by anxiolytic (e.g., diazepam, buspirone or ethanol) and increased by anxiogenic (e.g., caffeine) drugs (Steenbergen et al., 2011). Such dark avoidance behaviors have also been demonstrated in other fish species, including mosquitofish (*Gambusia holbrooki*; Maximino, Marques de Brito, Dias, Gouveia, & Morato, 2010). The sensitivity of zebrafish models to anxiotropic drugs (Maximino, da Silva, et al., 2014) suggests their reasonable predictive value, implicating both crayfish and zebrafish as potential models for anxiety-like states and the optimization of CNS drug screening.

3.2 | Aggression

Aggression has long been studied in aquatic invertebrates (Bovbjerg, 1956; Dingman et al., 2009; Sato & Nagayama, 2012; Tierney, Greenlaw, Dams-O'Connor, Aig, & Perna, 2004). In crayfish, aggressive and social behaviors are usually assessed during dyadic agonistic encounters, often with overt dominance-subordinated relationships (Bovbjerg, 1956; Dingman et al., 2009; Issa et al., 1999; Moore, 2007; Sato & Nagayama, 2012; Tierney et al., 2004). Behavioral endpoints in this test vary from low-stress (decreased approaches to a potential opponent) to high-stress (unrestrained fighting with attempts to remove the chelae or legs of the opponent) (Huber & Delago, 1998). Fighting usually stops when one individual retreats (using a tail flip) or crawls away from the opponent (Bruski & Dunham, 1987).

In zebrafish, multiple paradigms have been used to elicit and assess aggressive behavior (de Abreu et al., 2019; Zabegalov et al., 2019). For example, a widely used assay is the mirror test (Barbosa, Lima-Maximino, & Maximino, 2019; Gerlai, Lahav, Guo, & Rosenthal, 2000; Giacomini et al., 2016), where aggressive behavior is evoked by presenting fish with a mirror, typically placed on one side of the tank at an angle (Figure 1). The interaction of the fish with its own image is recorded after a short acclimatization period (Norton et al., 2011). To score aggression, the tank can be virtually divided into equal segments, and time spent near the mirror, as well as time spent in aggressive display, is assessed as an index of aggressive motivation (Way, Ruhl, Snekser, Kiesel, & McRobert, 2015). Displays are usually scored as the fish erecting its dorsal and anal fins and flaring its body flank toward the opponent. It is also possible to elicit aggressive displays by showing videos of conspecifics, evaluating aggressive behaviors (e.g., bites) and time spent in the area near the video stimulus (de Abreu et al., 2019; Way et al., 2015; Zabegalov et al., 2019). Although both models elicit aggressive displays in zebrafish, because the animal is unable to interact with the opponent, such aggressive behavior does not follow the usual escalation observed in natural contexts. Thus, interactions with conspecifics (e.g., dyadic fights between size-matched males) to elicit the complete aggressive repertoire from both appetitive (display) to consummatory (fight) components (Dahlbom, Backström, Lundstedt-Enkel, & Winberg, 2012;

Oliveira, Silva, & Simões, 2011; Teles & Oliveira, 2016), become necessary .

In dyadic behavioral assays, same-sex pairs of fish are typically placed into a tank, isolated by a removable opaque divider. After an overnight acclimation, the divider is removed, and the fish are left to interact for 30 min, which is usually sufficient to determine a clear winner. Behavioral patterns that can be observed include displays; circling (fish approach one another in opposite directions and with erected fins, and in an antiparallel position circle around each other usually ascending in the water column); strikes (fish swims rapidly toward the opponent but no physical contact occurs between them); bites (fish opens and closes its mouth in contact with the body surface of the opponent); chases (similar to strike behavior but with an active pursuit by the aggressor); retreats (fish swims rapidly away from the opponent in response to a strike or a bite); escapes (continued escape reaction in response to a chase); and freezing (fish stays immobile with all fins retracted) (de Abreu et al., 2019; Oliveira, Silva, & Simoes, 2011; Zabegalov et al., 2019).

3.3 | Sociality

The social domain has also been studied in aquatic invertebrates (Bovbjerg, 1956; Dingman et al., 2009; Sato & Nagayama, 2012; Tierney et al., 2004). Social interactions in crayfish are usually measured during dyadic agonistic encounters, sometimes during the establishment of dominance-subordinated relationships (Hayes, 1975; Huber & Delago, 1998). The mirror test has also been used to evaluate social response, in which an adult crayfish is placed inside a glass tank with a mirror, assessing rearing up (climbing the wall), turning, cornering (facing the corner for >5 s), backward walking, and crossing the midline of the aquarium (Drozdz, Viscek, Brudzynski, & Mercier, 2006). Crayfish behavioral responses seem to depend on prior socialization levels (Drozdz et al., 2006). Indeed, crayfish that had previously been housed in isolation show no difference in rearing, turning, cornering, or backward walking between the mirror and non-mirror portions of the tank (Drozdz et al., 2006). In contrast, crayfish housed in pairs increase all five behaviors in front of the mirrors (vs. in the non-mirror portions of the tank) and spend more time near the mirror (Drozdz et al., 2006), similarly to zebrafish, whose social isolation typically decreases shoal cohesion, likely due to the absence of social cues (Shams, Amlani, Buske, Chatterjee, & Gerlai, 2018). Together, these findings suggest that crayfish may as well be a suitable model organism for further social testing.

Several tests are widely used to assess social/agonistic behavior in zebrafish beyond aggression (Barba-Escobedo & Gould, 2012; Engeszer, Ryan, & Parichy, 2004; Gerlai et al., 2000; Muto, Taylor, Suzawa, Korenbrot, & Baier, 2013). For example, zebrafish social preference can be tested in a tank positioned between two other tanks, one empty and another containing a single conspecific (Barba-Escobedo & Gould, 2012) or a group of zebrafish (Giacomini et al., 2016). Fish are acclimated to the tank before behavior is recorded, and the videos are then analyzed, assessing time spent in proximity to the conspecifics (Barba-Escobedo & Gould, 2012; Giacomini et al., 2016). The shoaling test has also been used to assess sociality in fish (Miller & Gerlai, 2007, 2011). In this test, animals are analyzed in groups, assessing inter-fish distance, nearest and/or farthest neighbor distance, and/or shoal area (Green et al., 2012; Miller & Gerlai, 2007). However, this test does not strictly measure social preference per se, and is sensitive to changes in other behavioral domains (e.g., anxiety-like behavior), since, for example, anxiety naturally increases shoal cohesion in zebrafish (Engeszer et al., 2004; Miller & Gerlai, 2007).

3.4 | Neural mechanisms in stress and affective behaviors

In crayfish, stress-related behavior has been linked to altered serotonin signaling (Fossat et al., 2014). For example, stressing crayfish via electric shocks (Fossat et al., 2014, 2015) or by lowering their social status (Bacqué-Cazenave et al., 2017), seems to increase anxiety-like behaviors, an effect that is mimicked by injecting serotonin into crayfish hemolymph (Fossat et al., 2014; Table 1). Serotonin also triggers crayfish aggression (Tierney et al., 2004), possibly by reducing the likelihood of retreating and by increasing fight duration (Huber & Delago, 1998), thus, evoking a pro-aggressive and anxiogenic profile. Crayfish social status is usually established in dyadic fights (winner vs. loser) with physically larger animals more likely to become winners, however, when injected with serotonin, smaller crayfish are successfully able to win these confrontations against larger untreated crayfish (Momohara, Kanai, & Nagayama, 2013). Moreover, larger crayfish injected with octopamine also lose when set against untreated smaller animals, while wining by dominant crayfish is prevented by mianserin, an antagonist of serotonin receptors, and reinforced by fluoxetine (Momohara et al., 2013). However, current knowledge of socio-positive behaviors and their modulation by the serotoninergic system in crayfish is still limited, meriting further studies.

Analyses of zebrafish anxiety-like (Egan et al., 2009; Maximino & Herculano, 2010), aggressive (Norton & Bally-Cuif, 2012; Zabegalov et al., 2019) and social behaviors (Soares, Cardoso, Carvalho, & Maximino, 2018) strongly implicate the serotonergic system is modulating fish affective behaviors (Table 2). This system is particularly relevant, because albeit not fully conserved in terms of neuroanatomy and genetics (Herculano & Maximino, 2014), it is functionally associated with emotional domains across vertebrates and invertebrates (Curran & Chalasani, 2012; Herculano & Maximino, 2014; Mohammad et al., 2016). Zebrafish anxiety-like behavior is usually affected by serotonin in a receptor-dependent manner (Herculano & Maximino, 2014; Maximino, Lima, Costa, Guedes, & Herculano, 2014; Nowicki, Tran, Muraleetharan, Markovic, & Gerlai, 2014; Ogawa, Ng, Ramadasan, Nathan, & Parhar, 2012; Ponzoni, Daniela, & Sala, 2016). For example, serotonergic psychedelics, such as lysergic acid diethylamide (LSD) (Grossman et al., 2010), mescaline (Kyzar et al., 2012) and 3,4-methylenedioxymethamphetamine (MDMA;

TABLE 2 Selected examples of pharmacological modulation of zebrafish behavior

Drugs	Dose	Behavioral effects	References
Aggression			
Dizocilpine (MK-801)	5 μM	Reduced aggression	Zimmermann, Gaspary, Siebel, and Bonan (2016)
Ethanol	0.25, 10 and 20%	Increased aggression	Fontana et al. (2016), Sterling, Karatayev, Chang, Algava, and Leibowitz (2015)
Fluoxetine	50 μg/L	Reduced aggression	Giacomini et al. (2016)
	5 mg/L	Reduced aggression in dominants	Theodoridi, Tsalafouta, and Pavlidis (2017)
Anxiety			
O-Acetyl-L-carnitine	0.1, 1 and 10 mg/L	Anxiolytic effect	Pancotto, Mocelin, Marcon, Herrmann, and Piato (2018)
Amitriptyline	50 μg/L	Anxiolytic effect	Meshalkina et al. (2018)
Fluoxetine	0.1 mg/L	Reverted effects of unpredictable chronic stress (UCS)	Song et al. (2018)
LSD	250 μg/L	Anxiolytic effect	Grossman et al. (2010)
MDMA	40–120 mg/L	Anxiolytic effect	Stewart, Riehl, et al. (2011)
Mescaline	20 mg/L	Anxiolytic effect	Kyzar et al. (2012)
N-acetylcysteine	1 mg/L	Reverted effects of UCS	Mocelin et al. (2019)
Ibogaine	10 and 20 mg/L	Anxiolytic effect	Cachat et al. (2013)
Noribogaine	1, 5 and 10 mg/L	Anxiolytic effect	Kalueff, Kaluyeva, and Maillet (2017)
Scopolamine	120 mg/L	Anxiogenic effect	Volgin, Yakovlev, Demin, Alekseeva, and Kalueff (2019)
Lithium carbonade	100 mg/L	Anxiogenic effect	Zanandrea, Abreu, Piato, Barcellos, and Giacomini (2018)
Caffeine	100 mg/L	Anxiogenic effect	Egan et al. (2009)
Social preference			
Alcohol	0.25, 0.75 and 1%	Disrupted group cohesion	Miller, Greene, Dydinski, and Gerlai (2013)
Diazepam	16 μg/L	Decreased social interaction	Giacomini et al. (2016)
Fluoxetine	50 μg/L	Decreased social interaction	Giacomini et al. (2016)
Ibogaine	10 and 20 mg/L	Disrupted group cohesion	Cachat et al. (2013)
Ketamine	20 and 40 mg/L	Disrupted group cohesion	Riehl et al. (2011)
LSD	100 μg/L	Disrupted group cohesion	Green et al. (2012)
MDMA	80 mg/L	Disrupted group cohesion	Green et al. (2012)
MK-801	5 μM	Lower social interaction	Seibt et al. (2011)
Nicotine	4 and 8 mg/L	Disrupted group cohesion	Miller et al. (2013)
Proline	1.5 mM	Disrupted group cohesion	Savio, Vuaden, Piato, Bonan, and Wyse (2012)

Abbreviations: LSD, lysergic acid diethylamide; MDMA, 3,4-methylenedioxymethamphetamine.

Stewart, Riehl, et al., 2011), evoke anxiolytic-like effects in zebrafish, increasing top swimming in the NTT and decreasing dark preference in the LDT. Serotonin also lowers aggressive behavior (Barbosa et al., 2019; Norton et al., 2011) and increases social preference in zebrafish (Barba-Escobedo & Gould, 2012; Ponzoni, Sala, & Braida, 2016).

Importantly, distinct behavioral and molecular effects can be triggered by both acute (Abreu et al., 2015; Barbosa et al., 2019; de Abreu et al., 2014; Giacomini et al., 2016) and chronic (Egan et al., 2009; Marcon et al., 2016; Petrunich-Rutherford, 2019; Song et al., 2018) exposure to serotonergic drugs, suggesting pro-social, anti-aggressive and anxiotropic roles of serotonin in zebrafish. In rodents, the serotonergic system also modulates anxiety (Broekkamp, Berendsen, Jenck, & Van Delft, 1989; Griebel, 1995; Sánchez & Meier, 1997), aggression (Chiavegatto et al., 2001; Ferrari, Palanza, Parmigiani, de Almeida, & Miczek, 2005; Olivier & Mos, 1992) and social behaviors (Dekeyne, Denorme, Monneyron, & Millan, 2000; Gemmel et al., 2017). For example, like zebrafish (Egan et al., 2009), rats chronically treated with fluoxetine display anxiolytic-like behavior and reduced behavioral responses to stress (e.g., reverting the suppression of exploration induced by stress; Zhang et al., 2000). In addition, 5-HT1A receptor agonists buspirone, ipsapirone and 8-OH-DPAT reduce aggression (Olivier & Mos, 1992) and a selective serotonin reuptake inhibitor (SSRI) citalopram impairs social interaction in rodents (Dekeyne et al., 2000). Therefore, zebrafish and rodents present rather similar effects of serotoninergic modulation of emotional behaviors.

While we mostly focus here on serotonin as a well-studied brain neurotransmitter involved in behavioral modulation in multiple species, other neurotransmitter systems that regulate affective behaviors in various species involve the noradrenergic, dopaminergic and gamma

aminobutyric acid (GABA)-ergic systems. For example, exposure to chlordiazepoxide, a GABA-ergic benzodiazepine ligand, reverts anxiety-like behavior in crayfish caused by stress (crayfish submitted to varying electric fields; Fossat et al., 2014) independently of changes in monoamine levels (Fossat et al., 2015). Crayfish exposed to 434 mM ethanol show hyperactivity (Blundon & Bittner, 1992), whereas injection of dopamine increases crayfish swimmeret beating (Tierney, Kim, & Abrams, 2003). Furthermore, aggressive behaviors in crustaceans involve motivation to engage in fighting, with winners presenting higher blood levels of dopamine and serotonin than losers (Sneddon, Taylor, Huntingford, & Watson, 2000).

Interestingly, the use of crayfish model systems has also demonstrated some promise in the study of the biological mechanisms of addiction (Alcaro et al., 2011) which are strongly implicated in behavioural deficits and stress (Sinha, 2008; Torres-Berrio, Cuesta, Lopez-Guzman, & Nava-Mesa, 2018). Indeed, crayfish exposure to cocaine, morphine and methamphetamine increases mobility (Imeh-Nathaniel et al., 2017), whereas exposure to D-amphetamine stimulates exploration (Alcaro et al., 2011). Finally, exposure of crayfish to morphine increases locomotor activity acutely but reduces it at higher and/or chronic doses (Dziopa et al., 2011).

TABLE 3 Selected open questions relevant to modeling affective and social disorders in vertebrates and invertebrates

Questions
How to develop crayfish and zebrafish assays that are most robust to study emotional disorders?
Are there individual differences in emotional behavior of both crayfish and zebrafish?
How does crayfish and zebrafish 'personality' contribute to the expression of emotional phenotypes?
Do emotional behaviors differ in both zebrafish and crayfish in strain- and sex-specific manner?
What is the role of epigenetic modulation of crayfish and zebrafish emotional deficits?
Are there structures in the zebrafish and the crayfish nervous systems that participate in the development of emotional deficits but do not have close analogues in humans?
How relevant are the existing behavioral assays in crayfish and zebrafish to mimick human emotional disorders?
Are there significant differences in traditional drugs' effects between crayfish, zebrafish and humans?
How can we objectively link quantitative characteristics of zebrafish and crayfish behavior to symptoms of human emotional disorders?
Is there any difference in emotional phenotypes presented by zebrafish and crayfish in natural habitat versus laboratory environment?
How can stress affect (or trigger) emotional phenotypes in crayfish and zebrafish?
How to develop crayfish and zebrafish models of emotional disorders that display sex differences in pathogenesis similar to those in humans?
Can computer technologies (e.g., behavioral visualization software) lead to automatic recognition and extraction of crayfish and zebrafish emotional behaviors?
Can current genetic tools (e.g., CRISPR) assist in the understanding of the mechanisms of emotional disorders in these two aquatic species?
What is the impact of gut microbiota on models of emotional disorders in crayfish and zebrafish?

Like crayfish, zebrafish are also highly sensitive to pharmacological modulation, with significant impact on anxiety-like behavior. For example, zebrafish also increase locomotor activity following D-amphetamine exposure (Irons, MacPhail, Hunter, & Padilla, 2010). They demonstrate anxiolytic effects following a 1-week ethanol treatment, increasing exploration and reducing erratic swimming (Egan et al., 2009). In moderate doses, alcohol enhances aggression and preference for conspecifics, whereas its high concentrations impairs these responses (Gerlai et al., 2000). Discontinuation of ethanol and morphine evokes anxiogenic-like behavior and elevated whole-body cortisol in zebrafish (Cachat, Canavello, et al., 2010). Such drug responses may also be influenced by sex, since cocaine withdrawal-evoked anxiogenic-like behavior develops earlier in female zebrafish, but is more robust and persistent in males (Patiño, Yu, Yamamoto, & Zhdanova, 2008).

Exposure to dexmedetomidine, an alpha-2 adrenergic receptor agonist, causes sedation in zebrafish (Ruuskanen, Peitsaro, Kaslin, Panula, & Scheinin, 2005), as do common GABA-ergic sedatives diazepam and barbiturates (Zhdanova, Wang, Leclair, & Danilova, 2001). In contrast, anxiogenic GABA-lytic drugs, such as ionophore channel blockers pentylenetetrazole and picrotoxin (Wong et al., 2010), or an inverse benzodiazepine agonist FG-7142 (López-Patiño, Yu, Cabral, & Zhdanova, 2008), predictably evoke anxiety-like behavior in zebrafish, paralleling their well-studied behavioral effects in rodents and humans.

Stress itself further modulates crayfish and zebrafish emotional responses. For example, zebrafish exposed to unpredictable chronic stress (UCS) increase aggressive response, whole-body cortisol levels (Rambo et al., 2017) and anxiety-like behavior (Marcon et al., 2016; Song et al., 2018). Acute stress elevates zebrafish aggressive and anxiety-like behavior, while decreasing social interaction (Cachat, Stewart, et al., 2010; Giacomini et al., 2016). In crayfish, acute stress also increases anxiety-like behaviors (Fossat et al., 2014, 2015). In turn, such evoked anxiety can be rescued by anxiolytic, antidepressant and antipsychotic drugs (e.g., benzodiazepines, SSRI, risperidone) (Fossat et al., 2014; Giacomini et al., 2016; Idalencio et al., 2015; Marcon et al., 2015, 2016).

4 | ECOLOGICAL IMPLICATIONS OF CRAYFISH AND ZEBRAFISH MODELS: FUTURE DIRECTIONS

As a model species, zebrafish is characterized by easy laboratory maintenance, short generation times, well-described genetics (Detrich Iii, Westerfield, & Zon, 1998) and detailed behavioral ethograms (Kalueff et al., 2013). Zebrafish mature at about 3 months in laboratory conditions (Eaton & Farley, 1974). Females can spawn every 1–6 days and a single clutch may contain several hundred eggs (Spence & Smith,

2006). Generation time is short, typically 3–4 months, and development is rapid, with larvae displaying food seeking and active avoidance behaviors within five days post fertilization, i.e. 2–3 days after hatching (Kimmel, Ballard, Kimmel, Ullmann, & Schilling, 1995). Mean life span of domesticated zebrafish is about 42 months, with the oldest individual surviving for 66 months (Gerhard et al., 2002). In the wild, individuals normally only live for one year (Spence, Fatema, Ellis, Ahmed, & Smith, 2007). There are also some key ecological implications in their behavioral output. For instance, zebrafish habitat includes shallow, slow-moving water with mud, sand/gravel, aquatic vegetation, and shelters from overhanging vegetation and/or banks (Parichy, 2015). The presence of vegetation has been associated with increased aggression in zebrafish in population-dependent manner (Bhat, Greulich, & Martins, 2015). For example, differences in feeding after disturbance have been observed between wild-derived and laboratory-reared zebrafish populations (Bhat et al., 2015).

From the ecological point of view, red-swamp crayfish has some added practical advantages (compared to zebrafish), including higher resistance to experimental manipulations and handling due to their larger size and hard exoskeleton. However, they also present some husbandry problems, such as considerable cannibalism in captivity (Stein, 1977) and higher aggression (versus other freshwater crayfish (Gherardi, 2013; Reynolds, 2011), thereby complicating their manipulation and laboratory use. Another advantage of using crayfish is the possibility of longer-term manipulation out of water, since this species is extremely resistant (physiologically and behaviorally) to air exposure stress (Banha & Anastácio, 2014; Ramalho & Anastácio, 2015). Although zebrafish are capable of surviving in hypoxic conditions (Rees, Sudradjat, & Love, 2001), low environmental oxygen concentrations can produce robust behavioral, physiological or biochemical deficits (Jensen, Nikinmaa, & Weber, 1993; Kramer, 1987; Kramer & Mehegan, 1981). Under ideal conditions the time to maturation in red-swamp-crayfish is 2 months and its generation time is 4.5 months (Huner, Barr, & Coleman, 1991). In the wild, their life span is up to 1.5 years but, in the laboratory, crayfish can live for 3–6 years (Huner et al., 1991). Depending on their size, females usually lay 100–500 eggs in each clutch and can reproduce more than once a year (Huner et al., 1991). Thus, crayfish arise as an important model for experimental studies due to their easy laboratory maintenance and high reproductive capacity.

Individual identification and labeling in the red-swamp crayfish is easier than in zebrafish, including subcutaneous injection of color dyes (Cheung, Chatterjee, & Gerlai, 2014), acoustic (PIT) tags (Cousin et al., 2012; Delcourt et al., 2018), binary-coded wire tags (Isely & Eversole, 1998), enumerated plastic streamers (Meriweather, 1986), oil-based permanent markers (Ramalho, McClain, & Anastácio, 2010) and cauterization applied to exoskeleton (Buřič, Kozák, & Vích, 2008). For a longer-term marking, implanting alphanumeric tag or visible implant elastomers (both applied under transparent ventral abdominal cuticle) or internal PIT tags (Buřič et al., 2008) have already been used, therefore making behavioral research of individual characteristic easier in this species.

Furthermore, somewhat differing from zebrafish, red-swamp crayfish have a remarkable tolerance to a wide array of ecological conditions (Huner et al., 1991), making them ideal for laboratory use. However, from the bioenvironmental perspective, some risks include escape and invasion of natural habitats, whose strong impacts have led to the inclusion of this species in several restrictive national or international legislations (Capinha, Leung, & Anastácio, 2011; Lodge et al., 2012; Souty-Grosset et al., 2016). Another ecological risk is the transmission of diseases or parasites to wild animals, even if the species itself does not escape the laboratory. The red swamp crayfish and other North American crayfish species carry the crayfish plague, a deadly disease whose transmission to wild populations of crustaceans is a serious concern (Svoboda, Mrugała, Kozubíková-Balcarová, & Petrusek, 2017). Finally, while other common crayfish species may represent potential candidates for laboratory use, they also pose higher ecological risks than the red-swamp crayfish. For example, *Procambarus fallax*, *f. virginalis* is a parthenogenetic (Martin, Dorn, Kawai, van der Heiden, & Scholtz, 2010), highly invasive crayfish (Chucholl, Morawetz, & Groß, 2012).

5 | CONCLUSION

In summary, studying affective behavior in both invertebrate (crayfish) and vertebrate (zebrafish) aquatic models may provide important insights into emotional responses and mechanisms underlying human affective illnesses, also fostering the discovery of novel drugs to treat these disorders (see Table 3). These animal models may also become important tools in the studies of emotional disorders due to their generally conserved genetic homology to mammals (Gutekunst et al., 2018; Howe et al., 2013; Shi et al., 2018). For example, crayfish—due to the underlying mechanisms which are strongly conserved—have recently emerged as a promising novel model organism in addiction research, showing sensitivity to human drugs of abuse (e.g., cocaine and amphetamine) in the conditioned place preference paradigm (Huber, Panksepp, Nathaniel, Alcaro, & Panksepp, 2011). Likewise, zebrafish have also been used to study addiction (Mathur & Guo, 2010; Schneider, 2017). For example, larvae pretreated with morphine prefer water containing morphine in a self-immersion test (Bretaud et al., 2007). Another key practical advantage of utilizing aquatic models, such as zebrafish and crayfish, is the use of immersion as route of administration, which remarkably facilitates low-invasive treatment, group medication (Treves & Brown, 2000) and increases the ease of drug dosing (Schroeder & Sneddon, 2017). Therefore, zebrafish and crayfish may also represent useful model organisms for bioethical research, utilizing less stressful and non-invasive procedures (de Abreu, Giacomini, Echevarria, & Kalueff, 2019).

In general, to better understand human emotional disorders, we may need to target not only specific individual phenotypes of interest, but also their neural aspects, such as neurochemistry or circuitry (Demin et al., 2019). Because no animal is a perfect replication of the human emotional landscape, not all criteria can be met by a single model of affective behavior (Demin et al., 2019). Thus, using a combination of different model organisms (e.g., rodents, zebrafish and crayfish) may improve our understanding of each specific emotional condition.

Despite all the advantages, these two aquatic models also present some limitations. For example, there are some discrepancies in

pharmacological effects on emotional behaviors, including anxiolytic (Hamilton et al., 2017), anxiogenic-like (de Abreu, Friend, Amstislavskaya, & Kalueff, 2018) or no effects (Cho, Lee, Choi, Hwang, & Lee, 2012) of scopolamine in zebrafish. In contrast, the effects of scopolamine on anxiety in crayfish are unknown. Serotonin exerts both anxiogenic- and anxiolytic-like effect in crayfish (Fossat et al., 2015; Trevor James Hamilton, Kwan, Gallup, & Tresguerres, 2016), while in rodents and zebrafish it has an anxiolytic-like action (Farhan & Haleem, 2016; Giacomini et al., 2016). One possible explanation for these differences may be genetic differences from mammals, including some duplicated genes (in zebrafish), so the combination of genetic components and the expression of these genes may result in distinct phenotypic responses, and may explain some of the varying responses to drugs when compared to humans and rodents (Gutekunst et al., 2018; Kalueff et al., 2014). Taken together, the evidence discussed here suggests both zebrafish and crayfish as promising experimental models of stress-related conditions, including anxiety, aggression and social deficits.

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Conceptualization, M.S.A., M.C.S., C.M. and A.V.K.; *Writing — Original Draft*, M.S.A., C.M., F.B., P.M.A., K.A.D., A.V.K. and M.C.S.

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